Blue Mountains Ash (*Eucalyptus oreades* R. T. Baker) in the western Blue Mountains

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Fire is an important factor in controlling the distribution of *Eucalyptus oreades* within its natural range in the western Blue Mountains. The species which is fire sensitive relies on seeding rather than resprouting after fire. In the western Blue Mountains, *E. oreades* produces annual rings in the wood, allowing the age of a tree and dates of fire damage to it to be determined. Stands of *E. oreades* thus allow establishment of a fire chronology in localized areas. In uniform-aged young stands which are undergoing self-thinning the suppressed individuals set seed before the dominant individuals. Trees which survive to become mature are less susceptible to fire damage, developing a bark skirt at the base which protects them from ground-fire damage. The trees enter the high fire risk period of summer with substantial seed reserves stored in capsules in the canopy. Wind-throw is a major cause of death of old trees, already fire- and/or termite-damaged.

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INTRODUCTION

Eucalyptus oreades R. T. Baker, (Blue Mountains Ash), also known as smooth-barked Mountain Ash or White Ash, occurs on plateaus, ridges and in gullies in the Blue Mountains of N.S.W. It is valued locally not only as a beautiful tree but as a species of economic importance. Pole-sized saplings are logged in Newnes State Forest to supply pit props for coal mining. The Explorers' Tree at Katoomba, marked by Blaxland's party when making the first crossing of the Blue Mountains in 1813 is *E. oreades* (Baker, 1919).

The vegetation of the Blue Mountains has been little studied despite the spectacular topography of the region and its proximity to the vast urban area of Sydney. For example, *E. oreades* is not even listed in a recent review of wet sclerophyll eucalypts on the east coast of Australia (Ashton, 1981). Apart from the original description of *E. oreades* (Baker, 1889) and more recent descriptions, with maps, of its Australian distribution (Boland *et al.*, 1984), no botanical publications deal in any detail with the species. Vegetation descriptions of the Mt Wilson area (Brough *et al.*, 1924; Petrie, 1925) include associations which contain *E. oreades* and recognize that aspect and altitude are important factors for its occurrence (Pidgeon, 1938). A vegetation classification of the western region of Sydney (Forster *et al.*, 1977), and the unpublished Forestry Commission 1:25,000 map of Newnes State Forest No. 748, set out its general distribution in the Blue Mountains.

Following studies on the ecology of wet sclerophyll species, particularly *E. regnans*, in Victoria and Tasmania (Ashton, 1958; Gilbert, 1959; Cunningham, 1960; Jackson, 1968), a picture emerged of the interdependence of tall eucalypt forest and fire, a picture which was not generally recognized by early workers on the forests of eastern New South Wales (Brough *et al.*, 1924; Petrie, 1925; Pidgeon, 1937, 1938, 1940; Beadle, 1954, 1962). The response of *E. oreades* to fire is well known in general terms to local staff of the

Forestry Commission and the National Parks and Wildlife Service but no information has been published on its response to fire or on its general biology.

As the urbanized area in the Blue Mountains expands rapidly, particularly along narrow ridges with an intrinsic high fire risk to property, there is increasing demand to minimize that risk by frequent burning, with little knowledge of its effects on the vegetation in general or on certain species in particular. Present-day attempts to manage fire in whole National Parks and in urban bushland areas represent a major change from earlier, more laissez-faire, approaches to fire control, an approach to fire which *E. oreades* survived. With the present trend towards planned intervention in previously unmanaged fire regimes, detailed information on the biology of the plants involved is clearly needed by land managers.

An additional threat to *E. oreades* is the discovery that the Newnes Plateau and adjacent high altitude areas contain huge deposits of sand and clay suitable for deep open-cut mining (Pecover, 1984; Anon., 1984). Implications for the landscape and vegetation of the western Blue Mountains region are severe.

This paper describes aspects of the distribution and life history of *E. oreades* which help to explain its occurrence in the fire-prone landscapes of the western Blue Mountains.

Distribution

General

Eucalyptus oreades occurs in a number of disjunct populations within the latitudes 28°15′S to 34°30′S (Fig. 1). The largest population is in the Blue Mountains. Other stands occur on the escarpment inland from Port Macquarie, in the Gibraltar Range between Grafton and Glen Innes, in the Binna-Burra—Springbrook—Mt Warning area near the New South Wales—Queensland border, and near Tenterfield (Boland *et al.*, 1984). The altitudinal range lies between about 700 and 1200 metres. The disjunct distribution could indicate a former, more continuous, distribution.

Blue Mountains

In the Blue Mountains, *E. oreades* occurs on sands and clayey sands derived from Triassic sandstone parent rock in the Katoomba and Grose soil associations (Forster *et al.*, 1977). It also occurs on alluvial and colluvial sands in valleys and deep river gorges, on cliffs, and on sandstone soils whose texture is influenced by deep, red clay loams derived from the basalt caps at Mt Wilson. It would appear that soil depth or type does not explain its distribution in the Blue Mountains.

A striking feature of the species' distribution in the Blue Mountains is its relationship to the spectacular topography. It occurs rarely on exposed ridges but is common on steep sheltered slopes with a southerly aspect and around the heads of valleys facing south and east, on cliffs and cliff ledges, and along creek beds (Fig. 2). In these locations it can occur as individuals, particularly on cliffs, or as dense stands in sheltered valleys (in wet sclerophyll or tall open-forest). On the gentler slopes of the plateaus and ridges extending west from Katoomba to the Newnes Plateau, mature trees develop spreading crowns with short boles and branches low down on the trunk. Such trees have been kept as specimen trees in the towns of the upper Blue Mountains. They also occur as widely spaced individuals in mixed eucalypt open-forest associations (dry sclerophyll). By contrast, trees growing in crowded stands on steep sheltered slopes develop straight tall trunks, topped by a simple domed canopy. These form stands of tall open-forest (wet sclerophyll). Trees growing on ledges and in joints on cliffs develop tall straight, often non-vertical, trunks.

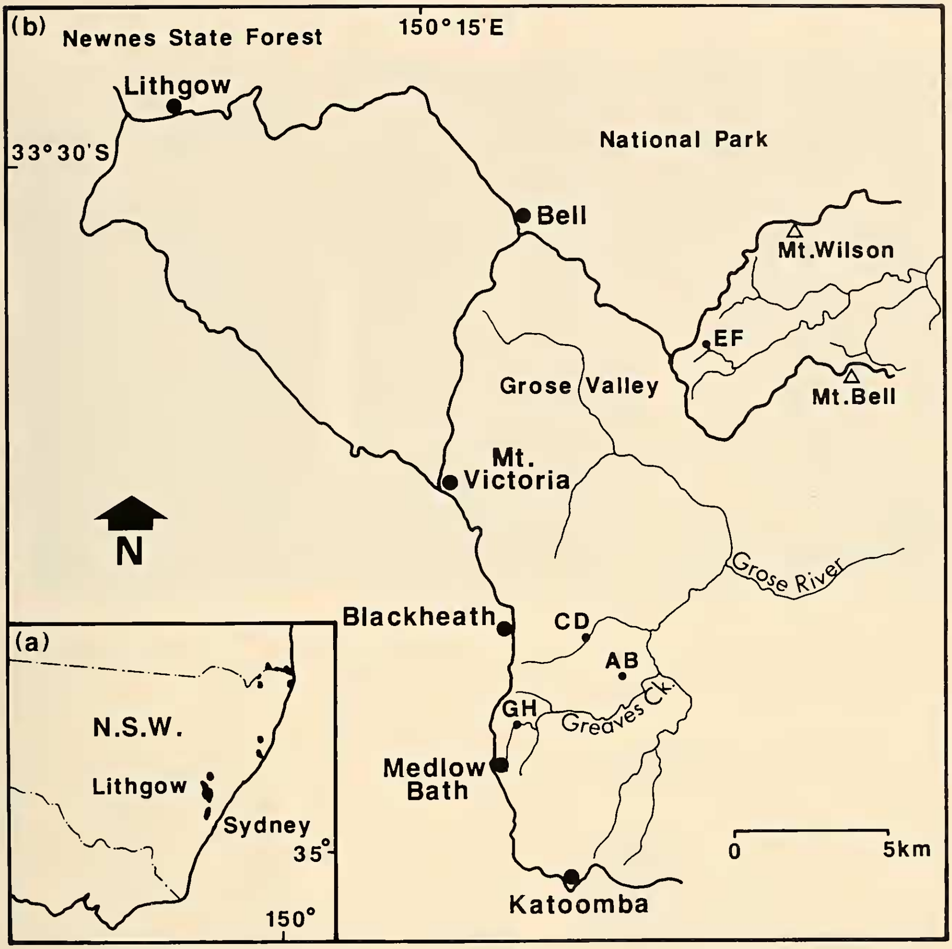

Fig. 1. **a**. General distribution of *E. oreades* (after Boland *et al.*, 1984). **b**. Location of sites in western Blue Mountains mentioned in text. More detailed locations specified in some diagrams.

Measured Transects

Fig. 3 is a downslope section through a tall open-forest of *E. oreades* at Evans Lookout near Blackheath. This site (AB) is typical of dense stands which occur on south-to-east-facing slopes of steep valleys (Fig. 2**b**), particularly near the main drainage lines. The site is below the rim of the plateau and above the first main line of cliffs within a tributary valley of Greaves Creek. An open woodland of eucalypts including *E. piperita* (Peppermint) and *E. sieberi* (Black Ash) grows on the plateau. Closed forest (rainforest) of mainly *Ceratopetalum apetalum* (Coachwood) and *Doryphora sassafras* (Sassafras) occupies the lower parts of the valley below the first main line of cliffs. At this site *Eucalyptus oreades* occupies the typical position of wet sclerophyll tall open-forest: relatively sheltered sites located between the even more sheltered rainforest vegetation below and the more exposed woodland vegetation on ridges and plateaus.

Beneath the *E. oreades* canopy is an open sparse intermediate canopy of *Acacia elata* (Cedar Wattle) and a lower dense canopy dominated by *Callicoma serratifolia* (Black

Fig. 2. **a**. Two large spreading *Eucalyptus oreades* trees on an exposed ridge, Gordon Lookout, Leura. **b**. Dense stand of *E. oreades* at the head of a south-facing gully near Evans Lookout, Blackheath (adjacent to transect at site AB, Fig. 3). **c**. *Eucalyptus oreades* trees on cliff face near Govetts Leap, Blackheath.

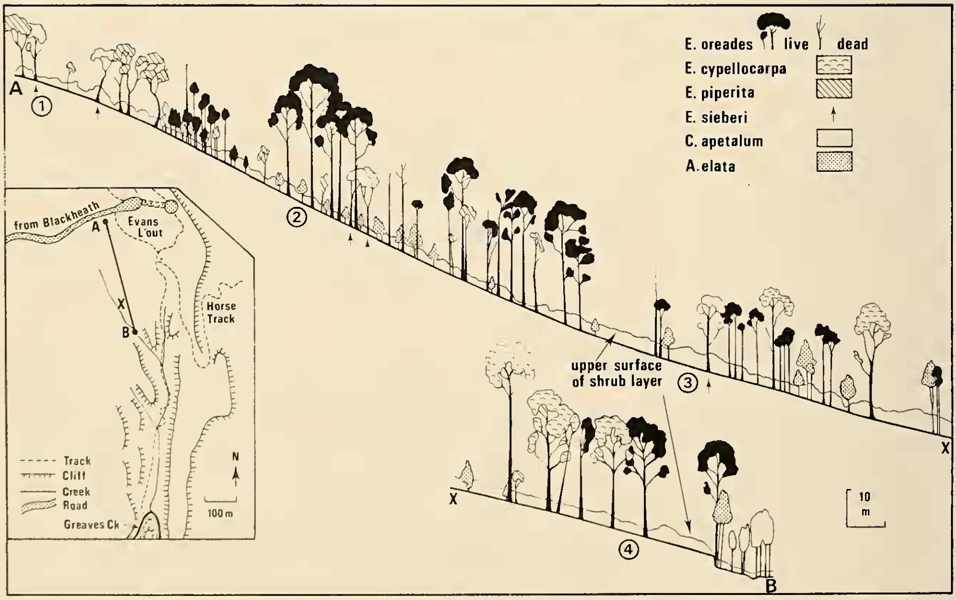

Fig. 3. Transect at site AB (1981) at Evans Lookout, Blackheath, showing distribution of *E. oreades* at the head of a south-facing valley, between dry sclerophyll woodland on plateau surface and rainforest in lower cliff-bounded valley.

Wattle). Dense clusters of ferns such as *Sticherus lobatus* and litter accumulations ensure very low light levels at soil level.

Fig. 4 presents similar data for two other valley slopes which face between east and south. Site CD is on an east-facing slope of the linear N-S valley of Govetts Leap Brook in an area dominated by woodland, shrubland and heath. Occasional tall trees of Blue Mountains Ash occur near the creek. Site EF, in the upper Bowens Creek Valley, is similar in situation to AB but EF was burnt in a severe fire in December 1979. Severe fire has probably not affected AB since 1959. In each site *E. oreades* clusters on sheltered moist slopes at the head of steep south-facing creeks beneath the scarp of a distinct ridge or plateau.

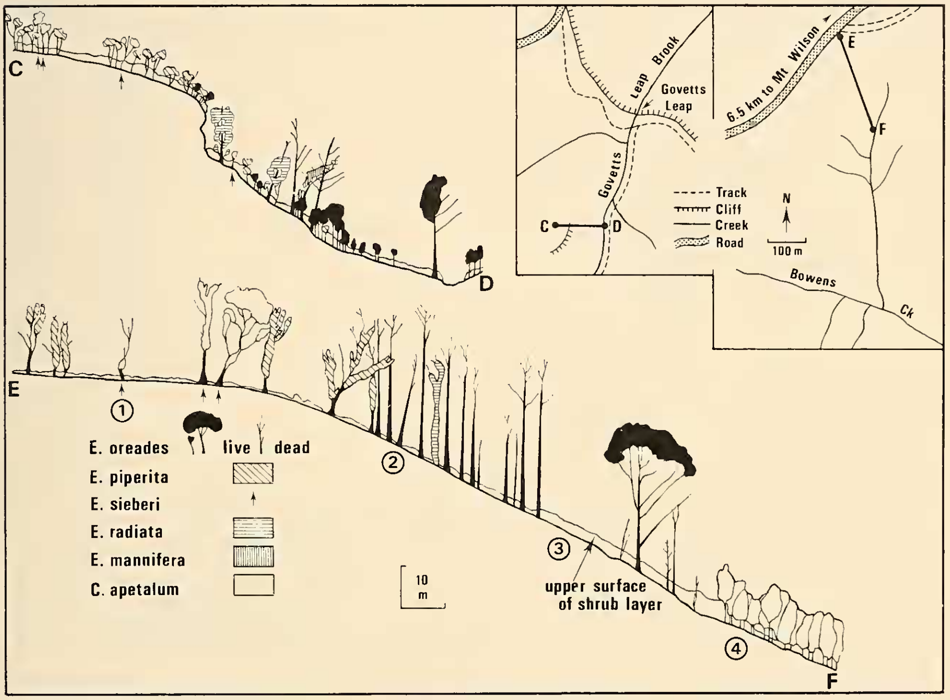

Fig. 4. Transects at sites CD and EF (1981). CD near Govetts Leap, Blackheath, shows live and fire-killed *E. oreades* in a small isolated stand last affected by fire in 1959. The site was again burnt in 1982 (see text). EF is a site where almost all mature trees in a large stand were killed by severe fire in December 1979. Extensive seedling establishment has since occurred.

Site GH (Fig. 5) traverses an asymmetric valley in the headwaters of Greaves Creek between Medlow Bath and Blackheath, where the Blue Mountains plateau is only slightly incised. Again, trees of *E. oreades* cluster on the east-facing steeper slope but widely spaced mature individuals occur in the woodland on the gentle slopes of the plateau. These tall trees project well above the other eucalypts and are usually associated with several small living or dead offspring.

Although the sites in Figs 3 and 4 contain trees of widely different size and age, similar individuals are often clustered. The patchy nature of the stands suggests episodic death and regeneration in response to fire as the causal process.

Effect of Fire on Stand Structure

Baker (1919) noted and we have confirmed that the wood of *E. oreades* grown in the Blue Mountains contained annual rings. Blue Mountains Ash also records fire damage in the wood where the vascular cambium is killed. Using fire scars dated from tree rings, a fire chronology was obtained for the sites AB, CD and EF and the ages of trees of various sizes were determined. Fig. 6a-c shows frequency distributions for tree size and the age and fire history of individual trees from these sites based on tree rings. The effect of fire is shown clearly at EF where the severe 1979 fire killed all trees below 0.5m stem diameter and many of those larger. These trees had survived fires in 1975, 1966 and 1959. At EF the survivors after the fire were a few large trees located downhill near the boundary of the closed forest. A swarm of seedlings established in the area occupied by the fire-killed trees and by December 1985 were up to 4m tall and sufficient in numbers to replace the earlier stand despite below average rainfall in 1981-1982 and several months of drought after the fire.

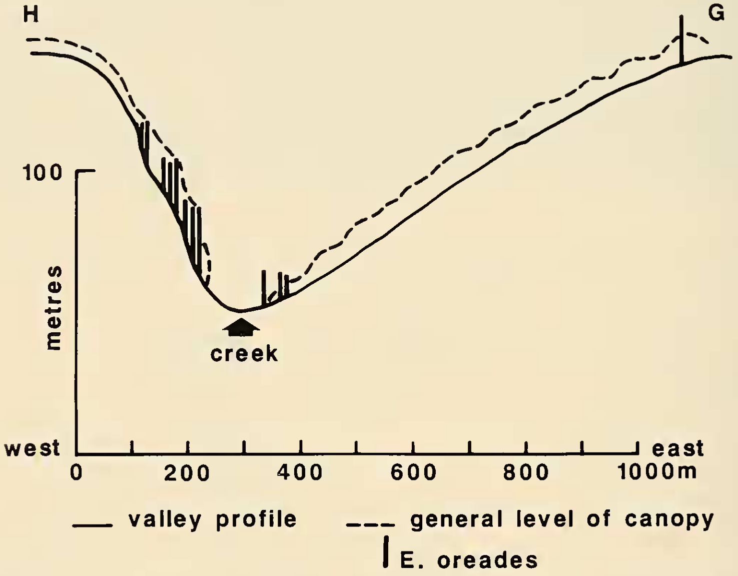

Fig. 5. Transect at site GH (1980), across upper Greaves Creek valley, between Medlow Bath and Blackheath, on the west of and parallel to electricity transmission line.

At Govetts Leap Brook (site CD) the swarm of small trees was killed in a severe fire of late 1982. The one large, mature tree survived but the fire killed half of its canopy and half of its vascular cambium to a height of 1.5m, severely weakening it. Since this fire, only 4 seedlings (up to 0.5m tall in December 1985) have become established.

At the Evans Lookout site (AB) a fire in 1959 was followed by the establishment of a cohort of trees dating from about 1960. This fire burnt patchily in the valley leading to localized death of trees, scarring of others, and the regeneration of new plants. A later less severe fire occurred in 1969.

Each site shows that fire easily kills young trees of *E. oreades* and severe fire, particularly through the canopy, easily kills mature trees. Following each fire there is usually recruitment of a new cohort of plants from seed, leading to the development of a mosaic of even-aged stands of different ages, each stand in its own burn patch. Observation of fire-damaged trees shows that fire kills the live bark and vascular cambium of trunk and branches and that the surviving parts of damaged trees have little capacity to resprout. This sensitivity of individual trees of *E. oreades* is in marked contrast to the vigorous resprouting after severe fire of most other eucalypts in the region.

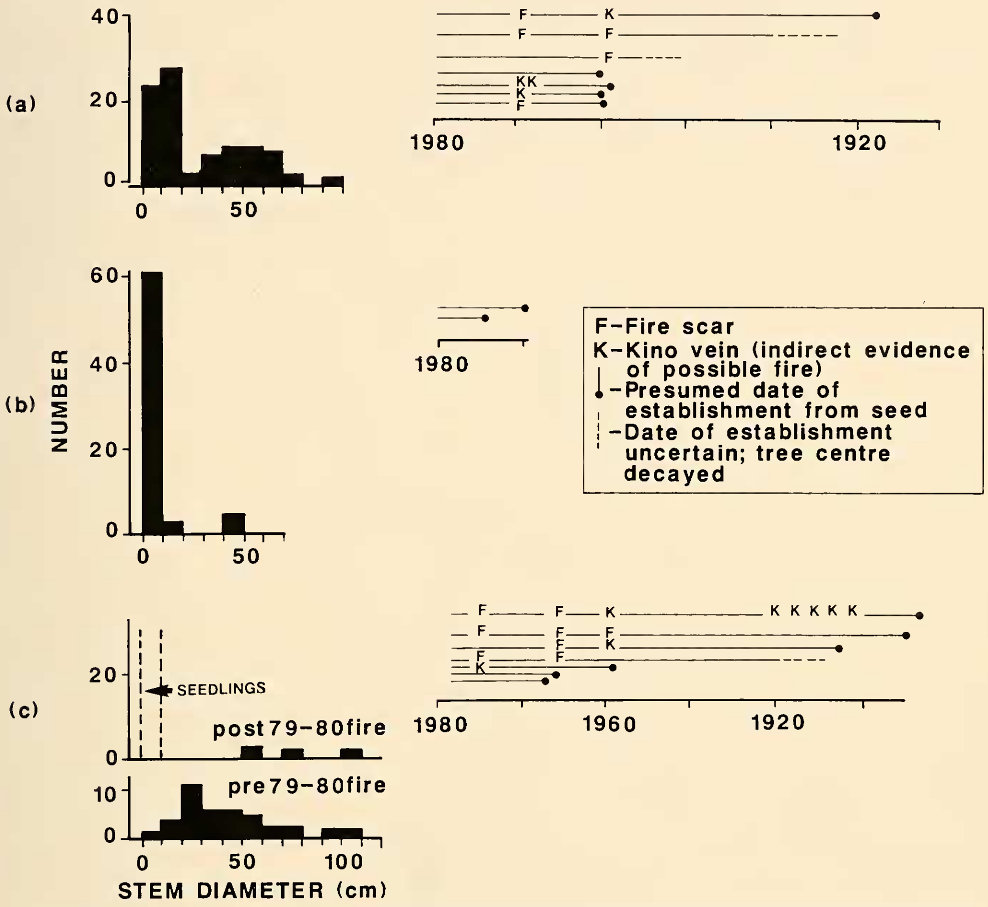

Fig. 6. Frequency distribution in mid-1980 of trees of various diameters with fire history of particular trees inferred from examination of annual rings and fire scars. **a.** Site AB Evans Lookout. **b.** Site CD Govetts Leap Brook. **c.** Site EF Bowens Creek valley.

Establishment of large numbers of plants following a fire leads to strong intra-specific competition and the development of a wide range of size within an even-aged stand. The dominant individuals grow rapidly; the suppressed individuals grow slowly and most die. Fig. 7 shows size classes in such a stand about 12 years after a fire. Trees ranged in height from about 2m to 8m. The most suppressed trees had very little (about 2cm) new growth per shoot, bore capsules from two years, buds and very few leaves. The dominant trees in the stand had extensive new shoot growth (about 30cm per shoot), bore no capsules or buds, and had a crown of dense foliage. After a further four years self-thinning had removed the smallest trees.

TABLE 1

Estimates from counted subsamples of number of buds, capsules, and seed stored in the canopies of three mature wind-felled E. oreades *trees*

	Total per tree						
(age in years)	Buds	Green capsules	Purple capsules	Grey capsules	All capsules	Fully viable seed	Viable seed per capsule
Tree 1 (>100)	24 000	10 000	9 000	2 000	21 000	63 000	3
Tree 2 (> 30)	60 000	36 000	1 000	6 000	43 000	128 000	3
Tree 3 (> 30)	111 000	24 000	4 000	4 000	32 000	96 000	3

Seed Production in Suppressed Trees

A striking feature is that the suppressed trees in the 12-year-old stand produced capsules whereas the dominant trees did not (Fig. 7). Each capsule contained about 3 viable seeds, a similar number to that of mature trees (Table 1). The total number of viable seeds per suppressed plant (average of about 350) was low because of the small number of capsules on each tree although the total number of seeds per unit ground area in the stand was approximately 36,000 per $100m^2$, a substantial fraction (about ⅓ to ½) of that found in a stand of mature trees because of the large number of suppressed plants. The early and effective reproductive behaviour of suppressed trees in a crowded uniform-aged stand constitutes a hedge against a severe fire in the period before the dominant individuals reach maturity. Diversion of resources from vegetative to reproductive growth in the suppressed trees guarantees their early death but provides an early seed bank at that particular site. This behaviour is an effective insurance against a severe fire following between about 10 and 25 years after an earlier one.

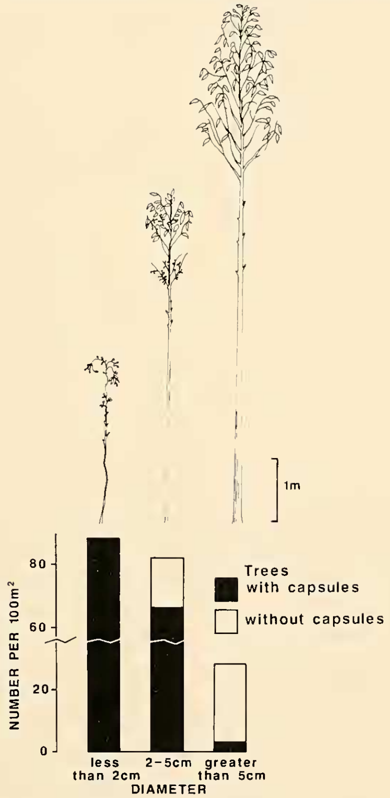

Fig. 7. Size distribution of a dense young stand of *E. oreades* regenerated after clearing and fire in 1969. Drawings are representative of three size classes. Stem diameter measured 10cm above ground level. Stand located at the head of a south-facing valley on the southern edge of the Katoomba Airfield (Medlow Bath).

Seed and Litter Production in Mature Trees

Mature *E. oreades* trees bore three distinct age classes of capsules, as well as developing buds (Table 1). The outermost growing tips of branches bear new vegetative growth and young flower buds which open in summer. Behind these, within the mature leafy area of the branch, are the green capsules from the previous summer's flowering. Further back is an area of small branches usually devoid of leaves which bear purple capsules which are two years old. Still further back on the branches are grey capsules borne either on persistent dead twigs or on the main branch itself. These grey capsules may be three years old or older.

Viability of seeds from the three colours of capsules is shown in Table 2. Only 2% of seeds from green capsules collected in August 1980 were viable, but by October, all ages of capsules contained viable seed. In all capsules larger, heavier seeds were more likely to be viable than smaller, lighter ones (Table 2). *E. oreades* therefore enters the high risk summer fire period with large amounts of viable seed stored in the canopy (Table 1).

TABLE 2

Percentage germination, and weight per seed, of three length classes of seeds from three capsule ages harvested in October 1980 from storm-felled trees
Germination was tested on four replicates of 25 seeds.
The standard errors are given in brackets

Capsule colour	Length of seed (l) longest axis (mm)	% germination	Average seed weight (mg)
green	$1.8 < l$	89 (±1)	1.9 (±0.02)
(from Jan 1980	$1.0 < l < 1.8$	59 (±3)	1.5 (±0.03)
flowering)	$0.7 < l < 1.0$	3 (±1)	1.0 (±0.02)
purple	$1.8 < l$	65 (±5)	1.7 (±0.08)
(from Jan 1979	$1.0 < l < 1.8$	51 (±3)	1.3 (±0.04)
flowering)	$0.7 < l < 1.0$	0	0.9
grey	$1.8 < l$	45 (±14)	1.3 (±0.15)
(from Jan 1978	$1.0 < l < 1.8$	25 (±2)	1.0
or Jan 1977	$0.7 < l < 1.0$	1	0.8 (±0.02)
flowering			

Measurements of litter fall (Fig. 8) show the sequence of flowering and capsule development. Flower buds begin development enclosed within two bracts. These bracts are shed mainly in late summer to autumn, although some persist till October. Following bract fall the buds develop further and flowering takes place from mid-January to February. Observations of stands at many sites on the Blue Mountains plateau showed that flowering was synchronous within this period. Flowering occurs as the opercula of the buds fall off (Fig. 8). During flowering and immediately following it, many flowers and immature capsules fall to the forest floor. This is followed by a peak in seed fall during March and April. The seed fall peak precedes the later capsule fall peak, suggesting that seed is released from capsules within the canopy, not from fallen capsules. There is a peak capsule fall in May, the capsules on twigs falling in large numbers. These capsules are mainly purple capsules, although some grey ones fall as well. Each year the grey population is augmented by the purple capsules which escape falling in autumn.

RESPROUTING

The feeble resprouting of burnt *E. oreades* trees contrasts with the vigorous regrowth of other species. Even when the bark and vascular cambium remain alive few epicormic shoots are produced.

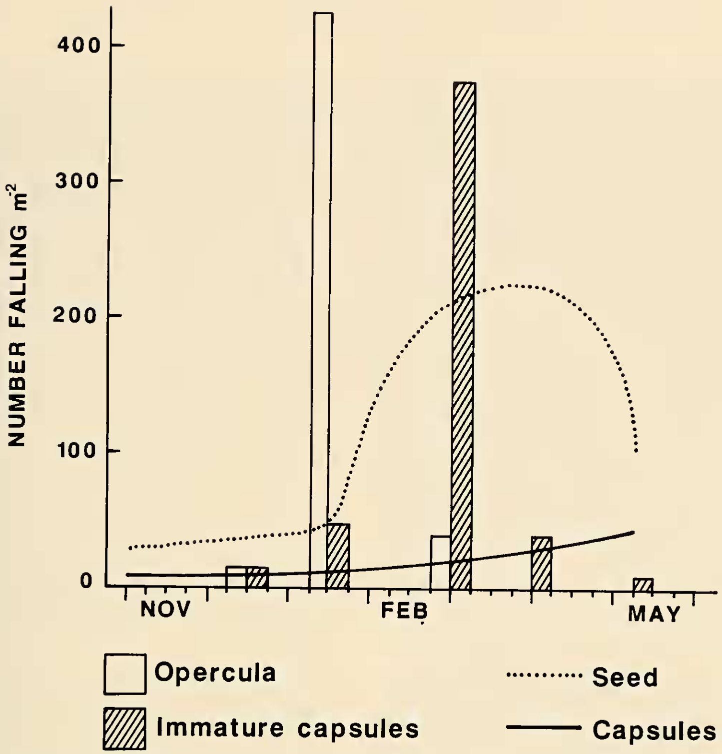

Fig. 8. Seasonal fall of reproductive parts of *E. oreades* in a dense stand (approx. 1000 live trunks of total basal stem area $54m^2$ per hectare). Values are means from 5 traps, each $1m^2$ in area.

A defoliation experiment was conducted to compare the resprouting ability of *E. oreades* with that of two vigorously resprouting species that grow in the same area. *E. piperita* and *E. sieberi* (Fig. 9). *E. oreades* produced significantly less resprouting than the other two species. Additionally, *E. oreades* was slower to produce sprouts than the other two species. Most of the refoliation in *E. piperita* and *E. sieberi* was confined to the top half of the stem while the foliage on *E. oreades* was more uniformly distributed over the whole stem, presumably an inefficient strategy for reestablishment of an upper canopy.

Although the number of resprouts is undoubtedly determined by the number of epicormic buds available, a feature not investigated, the lack of vigour of the shoots may be related to the lower levels of starch in the sapwood of this species in comparison with more vigorous resprouters (Table 3). Photosynthate is apparently devoted to growth in height, girth and canopy development rather than accumulation of starch reserves.

Fire Damage and Decay in Stems

Fig. 10 shows typical fire damage and subsequent recovery in stems of Blue Mountains Ash. Undamaged stems (Fig. 10a) show the regular annual increments of wood growth typical of rapid vertical growth where there is a distinct contrast in summer and winter temperatures. Unscarred trunks in mature trees are uncommon. Figs 10c and 10d show the effect of ground-fire on young saplings. Death of 50% of the circumference of young stems near ground level is common in surviving trees. If heavily damaged trees

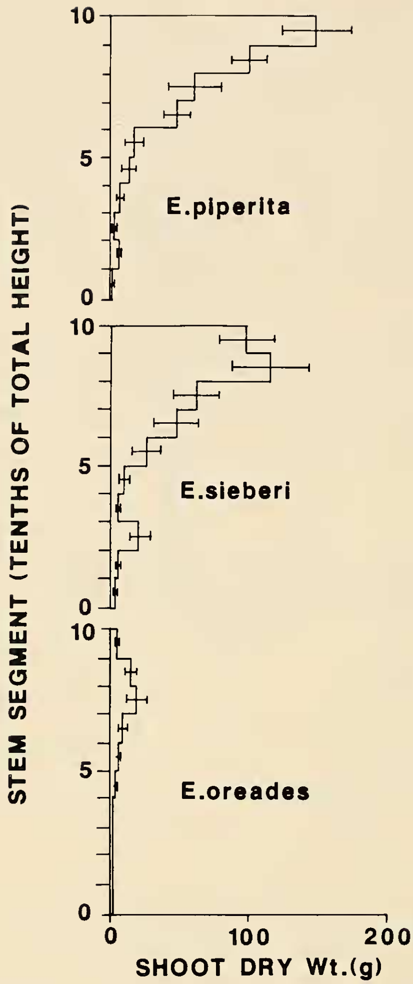

Fig. 9. Dry weight of shoots in each one tenth of stem height (mean of 7 trees) of *E. oreades* measured 143 days after artificial defoliation by pruning on 5 December 1980. Bars are standard errors of means.

TABLE 3

Mean percentage starch in breast height sapwood of three species of eucalypts at Medlow Bath in the Blue Mountains

All trees were about 10 yrs old. The mean is based on samples from six trees of each species taken 14.12.80. An analysis of variance showed a significant difference between the species ($p < 0.01$). Scheffe multiple comparison tests (Pollard, 1977) showed all species were significantly different ($p < 0.01$).

	Mean % Starch (± st. error)	
E. oreades	0.143	(± 0.02)
E. sieberi	0.725	(± 0.15)
E. piperita	1.525	(± 0.26)

survive, the fire scars become sealed within the trunk (Fig. 10**b**). Fire scars provide access for wood-decaying fungi and increase the possibility of fire burning into the centre of the trunk.

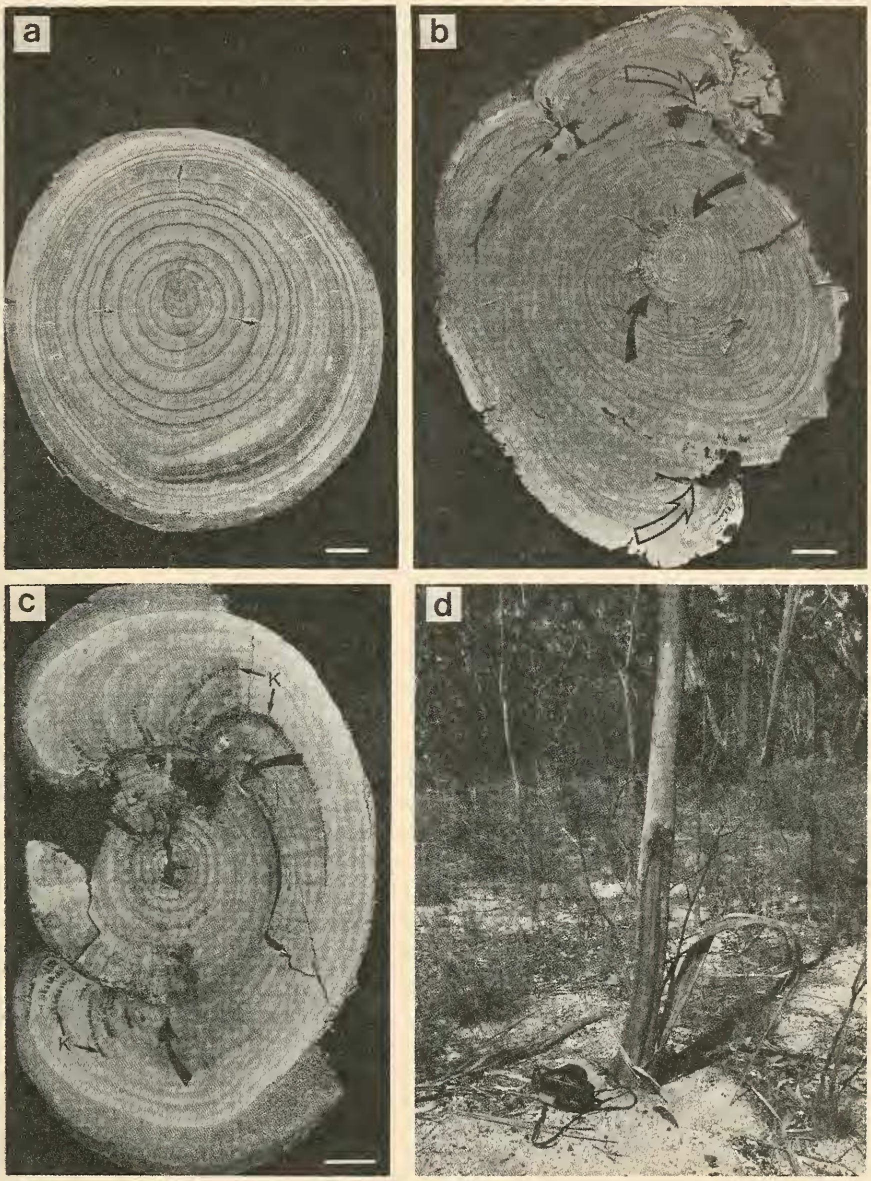

Fig. 10. Eucalyptus oreades. **a**. Cross section of undamaged trunk of tree. Annual growth rings are regular. Scale bar = 1cm. **b**. Cross section of trunk of fire-damaged tree. Cambium was destroyed by fire around ⅓ circumference (between solid arrows) when tree was about 10cm in diameter. This scar has been sealed by subsequent growth. More recently fire has destroyed cambium around nearly half the circumference (between open arrows). Scale bar = 5cm. **c**. Cross section of trunk of fire-damaged sapling. Cambium was destroyed by fire around more than half circumference (between arrows, to left). Subsequent growth has partially covered scar. Note kino veins (K) in wood. Scale bar = 1cm. **d**. Ground-fire has killed about half the circumference of young tree.

As a young tree, *E. oreades* is covered by thin moist live bark, some of which is shed annually. The importance of fire damage to the trunk of *E. oreades* is shown in Fig. 11 where a scheduled winter burn-off caused death to the trees or to sectors of the vascular cambium in trees younger than about 25 years old (15cm stem diameter). Protection from ground fire is provided by a basal skirt of persistent cork which starts to accumulate in trees aged about 20 years and older (Fig. 12). Large trees are afforded a high measure of protection from ground fires by the skirt although it is only effective with ground fires which do not rise high up the trunk. The annual decortication of bark contributes considerably to the fuel accumulation on the forest floor and in the canopy and increases the chance of fires spreading from the ground to the canopy.

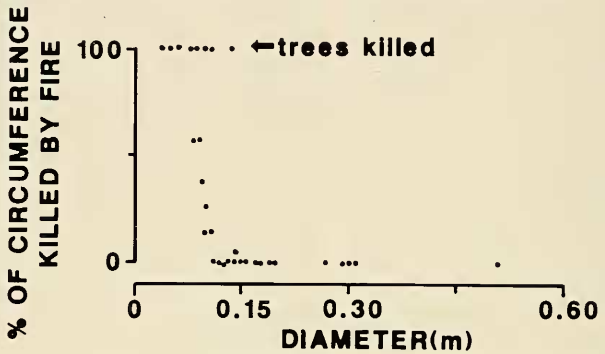

Fig. 11. Cambial death as percent of circumference of *E. oreades* trees at Medlow Bath in a scheduled winter burn in 1978. Measurements taken below 4m above ground level.

Internal decay of the trunks by fungi and termites occurs commonly and possibly in all very large specimens of *E. oreades*. Such decay can be inferred from external scars and fungal fruiting bodies, or directly from the presence of openings or pipes into the heartwood. Baker (1919) noted that the timber was particularly open-textured, that the fibres had delicate walls and large lumens and that the vessels were large and remarkably free from tyloses. Fungi and termites probably gain entry to the heartwood through fire scars such as those illustrated in Fig. 10. Trunks piped by fire are also a common feature (Fig. 13).

Wind Damage

Mature trees usually project well above the level of the surrounding canopy (Fig. 5) and are subject to severe stress from high wind. Strong winds commonly twist and break off the weakened stem well above ground level leaving a standing stump which does not regenerate. Fig. 13 shows a large emergent tree felled by a gale. The thin annulus of sapwood which supported the large canopy was only 4cm thick, the heartwood being completely burnt out.

Discussion

E. oreades is an excellent example of a tree species exhibiting rapid growth and relatively early death (Fig. 14). Dominant trees grow rapidly and achieve heights well above those of most other neighbouring eucalypt species. Suppressed trees grow slowly, become reproductive early and die prematurely but provide insurance against fires spaced about 10 to 25 years apart. Beyond about 25 years the dominant trees develop a seed bank in their canopies and a basal skirt of cork which protects them from ground-fires. Up to about this time all trees are extremely vulnerable to fires although the risk

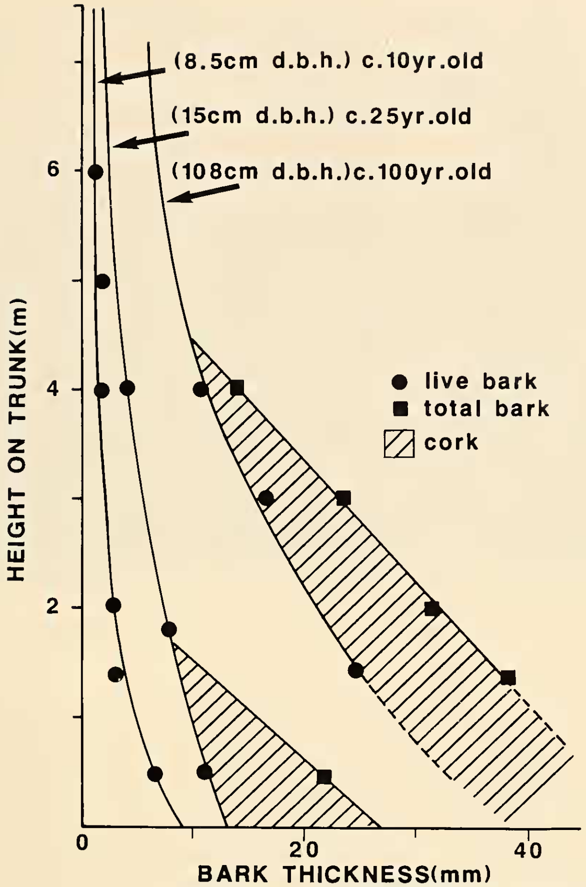

Fig. 12. Relationship between tree height and bark thickness for three *E. oreades* trees. d.b.h. = diameter at breast height. Cork refers to accumulated dead layers of tissue.

from canopy fires declines with tree age as older trees may be tall enough for their canopies to be above the burning zone. Progressive loss of strength in the heartwood makes mature trees that escape death from fire prone to wind collapse, the most likely cause of death of old trees.

E. oreades exhibits reseeding rather than resprouting in response to fire. The damaged plants die and replacement is from seed stored in the canopy. Attributes of the wood and bark, the early seed production of suppressed trees, seed storage in the canopy, rapid growth in height, absence of a lignotuber and sparse epicormic buds are all features appropriate to a reseeding response. Young trees establish from seed stored in the canopy which is shed after fire damage to the parent trees onto an ashbed with abundant light. Early growth of the tree is rapid so that it emerges above regenerating lower storeys of ferns, *Callicoma* and slower-growing trees. Rapid growth in height is an attribute of importance in the densely vegetated and shady south- and east-facing gullies. Regeneration was only observed after fire or other disturbance, such as clearing for transmission lines or landslip, which revealed bare soil and gave access to light. In effect, fire is probably the most important requirement for the establishment of new

Fig. 13. Stump of *E. oreades*, previously hollowed by termites and fire, broken off by wind. Trunk and upper branches on ground to right. Figures give scale.

individuals and stands, but an appropriate fire regime is required for their survival to maturity.

The response to fire by plants of different ages has implications for fire management of areas in which *E. oreades* grows. Complete exclusion of fires will prevent regeneration, shifting the vegetation towards rainforest. The species thrives in areas where occasional severe but patchy fires occur at intervals of several decades (possibly 50 years). Too frequent burning, even by low intensity winter ground fires will kill or excessively scar young trees and eventually prevent regeneration.

ACKNOWLEDGEMENTS

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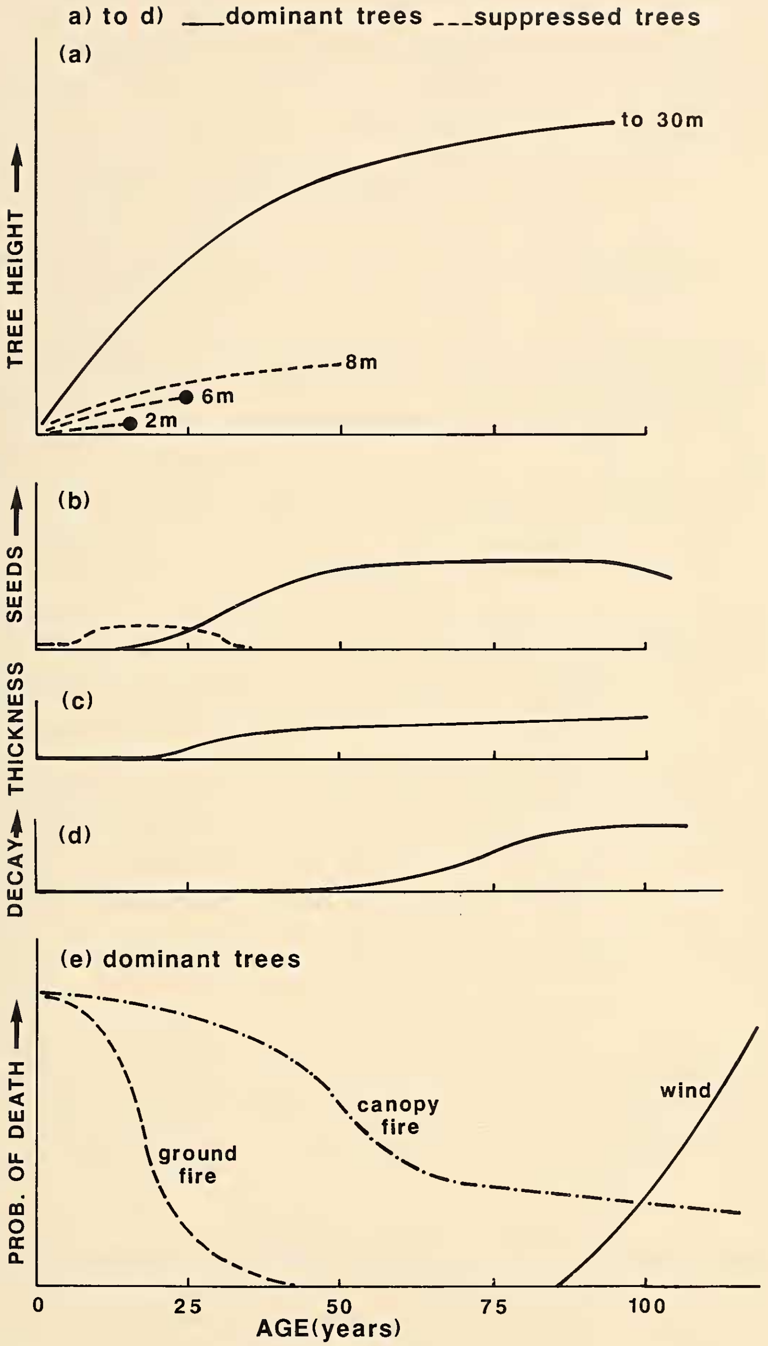

Fig. 14. Notional representation of events in life of *E. oreades* trees in a uniform-aged stand. **a**. Height of dominant and suppressed trees. • death of tree. **b**. Number of seeds per tree on dominant and suppressed trees. **c**. Thickness of cork on lower trunk of dominant trees. **d**. Extent of decay in heartwood of dominant trees. **e**. Probability of death of dominant trees from fire (ground or canopy) or wind throw (after initial piping of stem).

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